A COMPARISON OF MEASURED HEIGHTS AND DIAMETERS OF SELECTED YELLOW-POPLAR PHENOTYPES WITH EXPECTED HEIGHTS AND DIAMETERS BASED ON SOIL, TOPOGRAPHIC, AND CLIMATIC FEATURES

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by

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ABSTRACT

Eighteen superior phenotypes of yellow-poplar (*Liriodendron tulipifera*) were selected in four stands in southeast and east central Ohio. Selection criteria were superior height, diameter, and form characteristics. Four trees surrounding each select tree were chosen as comparison trees. Height and DBH were predicted for the select trees and comparison tree means, using regressions on soil, topographic, and climatic variables. When the residuals (predicted minus measured) were examined, both select and comparison trees were taller than expected, but the select trees exceeded their predicted heights by a significantly greater amount. Mean diameter residuals showed the select trees to be slightly larger than predicted and comparison trees slightly smaller; however, neither residual was significantly different than zero at the 0.05 level. A paired t-test of the select and comparison residuals of each plot did show a significant difference between the select and comparison tree diameters.

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INTRODUCTION

Tree improvement programs hold promise for increased yield and better wood qualities in commercial timber species. The first step in such a program is to select trees with the desired characteristics in natural stands to serve as seed sources. Selection is based on the appearance ("phenotype") of the candidate tree, usually compared with that of neighboring trees or with an average for the local region. It is hoped that a superior phenotype corresponds to a superior genotype, or genetic makeup, and that the characteristics will be passed on to the tree's progeny.

However, there is rarely a one-to-one correspondence between phenotype and genotype. In particular, environmental factors have a great influence on such characteristics as height, diameter, and tree form. It is not known if a tree is selected for its superior growth rate and form, or simply for its greater age or for better site conditions than its neighbors possess.

The effects of age and environment are partially offset by selecting in even-aged stands, and by selecting among trees on sites of relatively uniform quality. But without taking time-consuming measurements these effects are not fully known.

The purpose of this study is to evaluate the effectiveness of a simple phenotype selection. Selection consists of walking through a good stand of yellow-poplar (*Liriodendron tulipifera*) and picking the largest and best formed trees, without making corrections for age or environment.

Actual height and diameter are then compared with height and diameter predicted by regression equations for a tree of that age and on that particular site.

A second objective of the study is to test the regression equations, using plots other than those from which the equations were developed.

The results of this study can not tell us whether the selected trees are genetically superior, or that the next generation will inherit their superior characteristics. The genetic basis of these characteristics can only be determined by a progeny test, in which seed or cuttings of selected and control trees are grown in a uniform environment, and their performance in the desired characteristics is measured and compared with the performance of the parents. If, for example, the tallest offspring consistently come from the tallest parents, then inheritance of height can be inferred.

The applicability of the conclusions will be limited by the accuracy of the field measurements and of the regression equations used to predict height and diameter. In addition, only a very small portion of the total range of yellow-poplar is being sampled. The genetic variability and phenotypic expression of trees in southeastern Ohio, as well as the range of site and climatic factors, may not be representative of the species as a whole.

LITERATURE REVIEW

Yellow-poplar is a light-demanding species with excellent form, and grows rapidly on good sites. It is generally found in even-aged stands, either pure or in mixed hardwood associations, and is common on old-field sites. It grows best in sheltered coves in the southern Appalachians and in the Ohio River basin (Fowells 1965). On drier sites it may be unable to compete with upland species, and it has been found to be among the most sensitive to site quality of all the hardwoods (Della-Bianca and Olson 1961).

Many tree species have relatively low nutrient requirements, and studies have shown little relation between soil nutrient content and height growth. However, yellow-poplar is more nutrient-demanding than most species, and chemical factors have been found to be related to growth (Marquard 1978). Higher calcium and magnesium content of good yellow-poplar sites may be partly an effect rather than a cause, due to the high content of these nutrients in its leaves (Munn and Vimmerstedt 1980).

Studies relating site quality to soil, topographic, and climatic factors have been made for many tree species and regions of the U.S. (Carmean 1975). In most cases, once the effects of age are removed, the most significant factors affecting height growth are those that influence depth of the rooting zone and soil moisture availability. These factors include soil texture; depth to mottling, hardpan, or other restriction; and slope aspect, shape, and position (Carmean 1965).

Tree diameter is affected by the same factors as height. However, diameter is far more influenced by competition with surrounding trees for growing space (as expressed for instance by basal area of trees per acre) than is height (Spurr and Barnes 1980, pp. 300-302; Smith 1962, pp. 55-57, 265).

A general feature of soil-site studies and the resulting regression equations for predicting height growth is that they are most accurate when applied to relatively small areas with a narrow range of soil types and uniform climate (Della-Bianca and Olson 1961). Soil-site equations for yellow-poplar in southeastern Ohio are derived in Marquard (1978).

Many studies have shown little correlation between early height growth and site quality. Incidental factors affecting establishment and early growth, such as weed competition, planting techniques, or animal browsing, no longer influence growth once a certain height is reached (Brown and Stires 1981). For this reason I have used age at breast height (BH, 4½ feet above ground) and height above BH as parameters in this study.

Wilcox and Taft (1969) summarize the results of studies on the genetic characteristics of yellow-poplar. The tree has a large showy flower that is mainly insect-pollinated. Because of early flowering (before most pollinating insects are very active) and a self-incompatibility mechanism (seeds produced by self-pollination are inviable) only about 5% of the seeds are viable. Total seed production is very high, however.

Considerable variation exists between stands and among trees within stands for height growth and seed production. The results of controlled crosses show a good potential for improvement in growth (Wilcox and Taft 1969).

The first phase of a tree improvement program involves selecting trees with superior appearance from natural stands--phenotypic or mass selection. One method of selection is called individual-tree or baseline selection, in which a tree is selected if it exceeds by a certain amount the regional average for the desired characteristic. This method does not allow for the effects of site differences among stands, nor does it account for the age of the tree.

To correct for the effects of variations in site quality, comparison-tree selection may be used in even-aged stands. In this method the selected tree must score higher than surrounding trees (which presumably occupy sites of similar quality) by a given amount. A short-coming of comparison-tree selection is that trees close together are more likely to be closely related genetically than are trees far apart from each other. If superior trees occur in clumps rather than as isolated individuals they do not contrast as sharply, and genetic gain "might be as great from the relaxed procedure of choosing the best tree in a good stand without the expense of scoring it against comparison trees" (Ledig 1974).

Morgenstern _et al_. (1975) discuss plus tree selection, particularly as applied to conifer species. They conclude that phenotype selection (as modified by the results of progeny tests) can improve yield and quality characteristics, even in red pine (_Pinus resinosa_), a species known for its low genetic variability.

Pitcher (1982) evaluated phenotype selection in black cherry (_Prunus serotina_). The results of open-pollinated progeny tests at age 12 indicated that the geographic origin of seed was much more significant in determining progeny performance than was parental phenotype. He concluded that, while superior tree selection is an accepted technique in conifers, sampling from a wider population for provenance tests would do more to improve progeny performance in black cherry (and probably other hardwoods as well) than would putting a great deal of effort into locating superior trees.

The Ohio Agricultural Research and Development Center is conducting an improvement program in yellow-poplar in Ohio, using individual-tree selections from selected superior stands (mimeographed handout and personal discussion with Dr. Daniel Houston of OARDC).

METHODS AND MATERIALS

Establishing study areas

An attempt was made to include a variety of site consitions and genotypes by locating plots in several parts of the state. The time available for field work and analysis limited the number of stands that could be sampled and the total number of plots. In the end, 18 plots were located in three areas: 1-4 at the Barnebey Center (Fairfield Co.); 6-10 at Mohican State Forest (Ashland Co.); and 11-14 and 15-19 in two separate stands at Tar Hollow State Forest (Ross Co.). All three are in the residual soils area (unglaciated) of eastern Ohio.

Selection criteria

The selection criteria were established in consultation with Dr. Houston, who is conducting a survey of the range of genetic variation in growth rate and form of yellow-poplar in Ohio. "Superior stands" were chosen in the study area by visual inspection. Such stands must be located on good sites, relative to other sites in the area. Yellow-poplar must be the major component of the canopy, and the canopy trees should be relatively free of breakage and other forms of damage.

The candidate trees within the stands were chosen as "the best trees in a good stand." The greatest height and diameter were the main criteria for "best;" however, form characteristics (which determine the quantity and quality of hardwood lumber) were also important. A tree with good form could be selected over one that was larger, but poorly formed. The following is a list of the form criteria used, along with an explanation of the rationale for each. Trees were given a numerical rating for each characteristic, as indicated:

Height of clear bole, ft.	Reflects amount of clear lumber the tree will yield.
Merchantable height, ft.	Maximum height from which lumber can be sawed. Limit is either a large fork or branch, or 8-inch diameter.
Height to 8-inch top, ft.	Diameter limit of merchantable log.
Length of live crown, ft.	Vigorous trees have a larger live crown, usually 40-50% of total height.
Branch angle, degrees	As branch angle increases (branch becomes perpendicular to trunk) amount of wood affected by dead branch stubs is less, and stubs are healed over more quickly. Wide-angle branches also shed snow more easily, so are less subject to breakage.
Branch size (1=fine to 5=coarse)	Small branches have smaller knots, and heal more quickly so are less likely to allow decay organisms to enter.
Crooks (number of crooks to 4-inch top)	A crook usually represents a broken top at some time in the past. It affects the quantity and quality of lumber.
Sweep (1=none to 4=severe)	A curve in the trunk. It affects quantity and quality of lumber.
Epicormic branching (1=none to 3=severe)	Branches that sprout from dormant buds along the trunk, usually after an increase in light. Cause knots.
Branch scars (1=none to 4=large)	Large scars mean wood just under bark still has knot. Small scar indicates knot is deep, covered by clear wood.
Seed crop (1=heavy to 4=none)	Not a selection criterion; recorded to see if a relation exists between seed crop and other desirable characteristics.

Select trees within a stand were kept at least 75 yards apart, in order to minimize the degree of family relation between them. No one tree will be superior in all characteristics. In practice, the procedure was to find the largest trees in the stand, and select ones with a good rating in a majority of the form characteristics. In a few cases, trees with exceptional form were selected even though their height and diameter were less than that of other trees in the stand.

Six of the select trees were ones that had been previously selected by Dr. Houston. (Plots 1-3 correspond to 9A-1, 9A-3, and 9A-2; plots 12-14 correspond to 9B-1, 9B-2, and 9B-3.) The five trees at Mohican were selected by Dr. Brown and Chuck Vrotney. The remaining seven were selected by myself.

Comparison trees

Around each select tree the four nearest dominant or codominant trees were chosen as comparison trees. (A dominant is a tree whose crown is above the general level of the main conopy, and which receives full light from above and from the sides. Codominants are trees whose crowns make up the general level of the forest canopy; they receive full light from above and partial light from the sides.) Note that "comparison tree" is not used here in the same sense as in "comparison-tree selection," since these trees are not explicitly used in the selection process. They are chosen without regard to their form, except that they should be relatively free of wind or ice damage. Such damage might indicate that the tree's present height is not a full reflection of the growth potential of the site.

The comparison trees should also have been unsuppressed by taller neighbors at any previous time, another assurance that their present height will closely reflect site quality. These are the same criteria as those used in selecting trees for developing soil-site equations, or for determining site index from published curves. (Site index is the average height of free-grown dominants and codominants at a specified index age and is the most widely used means of indicating site quality in the U.S.) The past history of a tree is not known in detail, of course. However, a tree that has been severely suppressed is not likely to reach dominant or codominant status, especially in even-aged stands of a fast-growing, shade-intolerant species such as yellow-poplar.

Measurements

All height measurements were made with a Spiegal relaskop mounted on a tripod, and are given as height above breast height BH). Diameter at breast height (DBH) was measured to the nearest 0.1 inch using a diameter tape. An increment borer was used to determine age at BH. Stand basal area (BA, square feet per acre) was measured around each tree with a 10-factor wedge prism. The tree used as the center for each prosm plot was not included in the count.

For each 5-tree plot a set of soil and topographic features was measured. Slope azimuth (0-360°), slope shape (1=concave, 2=flat,3=convex), and slope percent were determined for the plot center. Total slope length and length above plot center (yards) were paced. Slope position was calculated as 100(length above plot/total slope length).

Two soil pits were dug on each plot (except in 3 cases, where only one pit was dug or else information from a neighboring plot was used) and values from the two were averaged. A soil profile description of each pit was made by Dr. Brown, with texture and depth recorded for the A1, A2, B1, B2, and B3 horizons. Samples from the A and the B2 were collected (samples from each of the two pits were mixed) for laboratory analysis of nutrient status (N, P, K, Ca, Mg, pH, cation exchange capacity, and lime test index), moisture retention, and percent sand, silt, and clay.

Regression equations for height and DBH

Marquard (1978) derived soil-site equations for height above BH of yellow-poplar in southeastern Ohio. Data from 96 plots were analyzed, including plots at Mohican and Tar Hollow. In his final equation, 20 selected soil, topographic, and climatic variables were screened for a best-fit equation, which I have used to predict heights in this study:

$$\begin{aligned}
\mathrm{LOG}_e\ (\text{tree height}) = \ & 4.1722 \\
& -15.705 \quad (1/\text{age}) \\
& +0.000603 \quad (\text{minor angle from southwest}) \\
& +0.000167 \quad (\text{total slope length}) \\
& +0.0365 \quad (\mathrm{LOG}_e\ (\text{slope position})) \\
& +0.00432 \quad (\text{thickness of B2 horizon}) \\
& +0.0547 \quad (\text{pH of A horizon})
\end{aligned}$$

$$R^2 = 0.778$$

Age clearly accounts for most of the variation in height. The other variables are ones that frequently appear in the literature on soil-site equations. The azimuth transformation gives northeast-facing slopes, which are generally the most favorable sites in regard to moisture stress and temperature extremes, the largest value, and southwest-facing slopes the lowest.

Marquard developed separate equations for plots north and south of Interstate 70, in addition to the one for all plots given above. The regional equations had higher R^2 values than the state-wide, but they were not used in this study for two reasons: my small sample sizes (5 north and 13 south plots) would have negated any gain in precision from using the regional equations; and the equation for the south plots was based on a relatively small number of plots that was not representative of the range of site conditions and combinations of factors found in the area.

Using Marquard's data plus an additional 30 plots located by Dr. Brown, I derived an equation for predicting DBH:

$$
\begin{aligned}
\mathrm{LOG}_e\ (\mathrm{DBH}) = {} & -2.4152 \\
& + 0.09599\ (\mathrm{LOG}_e\ (\text{age})) \\
& - 0.00147\ (\text{slope percent}) \\
& + 0.9362\ (\mathrm{LOG}_e\ (\text{height above BH})) \\
& - 0.00022\ (\text{slope length above plot}) \\
& - 0.00338\ (\text{total soil depth}) \\
& + 0.00365\ (\text{thickness of B2 horizon}) \\
& + 0.0776\ (\text{May to September precipitation}) \\
& - 0.0910\ (\text{May to June precipitation})
\end{aligned}
$$

$$R^2 = 0.862$$

Tree height was used as an independent variable in the diameter equation for several reasons. First of all, for the purposes of a scientific study it gives greater accuracy to the predictions. In a practical sense, tree height at some future age (for example, the site index base age) is often estimated for volume predictions. This height can then be used to estimate DBH at the same age and on the same site. With these two pieces of data, a more precise estimate of timber volume can be made, using tables that require both height and diameter.

The climatic data was compiled by Marquard from observations collected at weather stations nearest the study areas, published by the National Oceanic and Atmospheric Administration Environmental Data Service.

Only the two precipitation amounts entered the diameter equation at a significant level; other variables analyzed included average annual temperature, average May-June and May-September temperatures, average frost-free growing season, and average annual precipitation.

The negative coefficient for May-June precipitation seems to be at odds with common experience. The reporting stations are not very close to the study areas, so the published values may not accurately show precipitation in the forest. The discrepancy may also reflect an inverse relation between rainfall and number of frost-free days from north to south.

The negative coefficient for total soil depth is probably an artifact of the sampling process, in which some sites with shallow soils were particularly favorable due to other factors.

Basal area was last out of 64 variables tested in one-variable models for predicting DBH, and it was not among the first 30 variables to enter the multiple regression equations.

Soil moisture and texture values were unavailable at the time the equations were being run through the computer, so these variables were not included in the equation used for this study.

Data analysis

The major hypothesis to be tested is the null hypothesis that there is no difference between the measured heights and diameters of the select trees and the height and diameter predicted by the soil-site equations. The observed differences were tested for significance by paired t-tests, using expected and actual height or diameter for each plot as the paired measures. A separate test was made for the select trees and for the mean of the four comparison trees on each plot.

Comparisons between select and comparison-tree values are actually between a single observation and a mean of 4 observations. A set of means usually has less variability than a set of single observations. Since variability affects the magnitude of a t-value, on occasion a second t-test was made, between the mean of the 18 select trees and the mean of the 72 comparison trees, using the procedure for tests between samples of unequal size (Steel and Torrie 1980).

Simple correlations (R) were determined for branch size with height, DBH, and age. This test was made to see whether we were selecting trees that had small branches simply because they were smaller or younger trees, rather than trees with superior form.

Correlations were also calculated for basal area and height, DBH, and age. BA entered into the diameter regression at a very low level, which seemed to contradict common experience.

The accuracy of the equations in predicting height and DBH of the comparison trees was analyzed as a measure of their reliability. It provided a check on the equations with plots independent of those which had been used to derive the equations.

The diameter regression and statistical analyses were run under Release 79.5 of the Statistical Analysis System (SAS), at the Instructional and Research Computer Center of The Ohio State University.

RESULTS

Tree characteristics

Tables I and II summarize the observations made on the 18 plots. Under each characteristic a value is given for the select tree and for the mean of the four comparison trees on the plot. Paired t-tests were used to test the significance of the differences between select and comparison values.

In Table I note that, although the select trees had greater values for average age and for all heigh characteristics, the differences between select and comparison trees were significant at the 0.05 level or better only for DBH, total height, merchantable height, and height or 8-inch top. The mean basal area around the select trees is slightly less than that around the comparison trees; however, the difference is not significant at the 0.05 level. A t-test between 18 select and 72 individual comparison trees gave a similar result.

In Table II the means are in the direction of "better form" for the select trees in all 7 characteristics. However, the differences are only significant for crook, sweep, and branch scars.

TABLE I: Age, diameter, and height characteristics. (S = select tree; C = mean of 4 comparison trees)

Plot	Age (yrs.)		DBH (in.)		Total ht. (ft.)		Clear ht. (ft.)		Merch. ht. (ft.)		Ht. to 8" top (ft.)		Live crown (ft.)		Basal area (sq. ft./acre)	
	S	C	S	C	S	C	S	C	S	C	S	C	S	C	S	C
1	65	66	19.5	17.2	99	97	40	51	60	48	60	56	49	45	80	100
2	67	65.5	18.1	16.7	106	100	48	44	61	52	68	66	47	53	120	118
3	62	64	19.3	17.5	106	101	55	52	57	55	64	62	49	46	120	120
4	61	64	14.8	16.2	94	101	59	54	59	50	59	64	35	44	140	122
6	37	38	13.9	12.8	100	94	49	47	87	72	69	57	32	40	160	160
7	38	37.5	14.4	11.8	94	86	43	46	71	61	58	37	51	32	170	158
8	38	37.5	14.7	12.7	92	91	50	48	74	68	63	51	44	44	110	140
9	39	37	12.3	11.4	83	81	36	37	61	62	42	40	34	38	150	148
10	37	37	14.3	13.6	92	88	41	40	72	66	56	50	44	40	150	145
11	74	70.8	15.9	17.4	119	108	65	56	65	64	68	61	53	49	130	130
12	82	76	25.9	18.5	139	116	54	63	88	71	88	78	85	53	120	162
13	93	78.5	23.0	20.5	134	118	50	51	72	71	.	77	77	54	140	155
14	77	77.2	17.9	17.0	107	108	62	61	62	74	.	81	35	41	160	145
15	44	43.2	20.0	17.8	104	99	47	49	68	55	68	55	57	48	100	118
16	41	43	18.4	17.1	95	99	41	43	61	57	61	57	55	50	110	98
17	57	41.5	18.7	16.9	101	98	46	44	63	50	63	52	50	51	120	112
18	43	46.2	17.9	17.3	104	98	49	38	56	55	56	55	51	57	130	130
19	38	53.5	17.0	16.6	89	95	32	36	61	54	61	54	39	52	100	120
Mean	55.2	54.2	17.6	16.1	103.2	98.8	48.2	47.8	66.6	60.3	62.8	59.1	49.3	46.5	128.3	132.3
Mean of S - C	0.9		1.5		4.4		0.4		6.3		6.2		2.8		-3.9	
Std.err.	1.58		0.441		1.723		1.28		1.65		1.80		2.81		3.91	
$\hat{t}$	0.58		3.399		2.579		0.304		3.79		3.70		1.00		-1.10	
sign.	0.57		0.003		0.02		0.765		0.001		0.002		0.327		0.469	

TABLE II: Form characteristics. (S = select tree; C = mean of 4 comparison trees)

Plot	Branch angle, ° S	Branch angle, ° C	Branch size S	Branch size C	Crooks S	Crooks C	Sweep S	Sweep C	Epicormic branches S	Epicormic branches C	Branch scars S	Branch scars C	Seed crop S	Seed crop C
1	45	41	3	2.75	0	3.0	1	1.5	1	2.25	1	2.0	2	2.75
2	35	54	2	2.5	0	1.0	1	1.0	1	1.75	2	2.0	4	1.67
3	50	45	3	2.75	0	1.0	1	1.25	2	2.5	1	2.0	3	3.75
4	40	51	1	2.75	0	0.75	1	1.75	1	1.75	1	1.5	1	2.25
6	.	.	2	2.0	1	2.0	1	2.25	1	1.5	2	2.25	.	.
7	.	.	3	2.25	1	1.0	2	2.75	1	1.25	3	2.5	.	.
8	.	.	3	3.0	0	2.0	2	2.75	3	2.25	3	2.75	.	.
9	.	.	2	3.0	0	0.75	2	2.75	2	2.75	2	2.75	.	.
10	.	.	3	2.75	3	0.75	1	2.25	2	2.0	2	2.75	.	.
11	65	50	1	2.25	0	2.25	2	2.0	1	1.0	2	1.5	.	.
12	45	44	4	2.75	0	1.25	1	2.5	1	1.25	1	1.5	.	.
13	60	50	2	2.75	2	1.5	3	2.25	2	1.25	2	2.0	.	.
14	50	48	4	3.0	1	1.5	1	1.75	1	1.0	1	1.0	.	.
15	45	40	4	2.25	1	1.5	1	1.5	1	1.25	3	2.5	.	.
16	50	42	3	2.75	0	0.75	1	1.0	2	1.25	2	2.75	.	.
17	40	46	2	2.0	1	0.75	1	1.25	1	1.5	2	2.25	2	2.5
18	40	40	2	1.75	0	1.5	1	1.75	1	1.0	2	2.75	2	2.0
19	45	36	1	2.5	0	1.0	1	1.25	1	1.0	3	3.25	.	.
Mean	46.9	45.2	2.5	2.5	0.6	1.4	1.4	1.9	1.4	1.6	1.9	2.2	2.3	2.5
Mean of S - C	1.7		-0.04		-0.8		-0.5		-0.2		-0.3		-0.15	
Std.err.	2.56		0.22		0.27		0.12		0.13		0.12		0.30	
$\hat{t}$	0.69		-0.19		-2.94		-3.90		-1.49		-2.33		-0.5	
sign.	0.503		0.854		0.009		0.001		0.154		0.033		0.634	

Predicted total heights

Table III gives the predicted height, measured height, and the residual (predicted - measured) for the 18 select trees and 18 comparison tree means. All but one of the residuals are negative, indicating that the predicted heights are too small. The t-values of the residuals are large, for both sets of trees. The comparison trees show a larger (more negative) t-value (indicating that the sample mean is farther from the hypothesized population mean u=0), even though the mean residual is greater for the select trees (-14.3 feet) than for the comparison trees (-9.8 feet). The reason for this apparent contradiction is the lower variability in the comparison tree values, because each one of these values is actually a mean of four heights. The standard deviation of the 72 individual comparison tree heights is 7.56, rather than 5.71 for the 18 mean heights.

More information can be extracted from the data by two other tests:

1. A pairwise comparison of select and comparison (4-tree mean) residuals. This test shows the mean select height residual to be greater, with a significance of 0.01.
2. A comparison of two means of unequal sample sizes (18 select and 72 comparison tree residuals). The result of this test also indicates that the mean of the select height residuals is significantly greater than the mean of comparison height residuals, at a level of 0.046.

In summary, the select trees exceeded their predicted heights by a significantly greater amount than did the comparison trees.

TABLE III: Predicted heights and height residuals (predicted - measured).

Plot	Height of select trees (ft.)			Mean height of comparison trees (ft.)		
	Predicted	Measured	Residual	Predicted	Measured	Residual
1	93.3	99	- 5.7	93.6	97.0	- 3.4
2	100.4	106	- 5.6	99.9	100.5	- 0.6
3	97.7	106	- 8.3	98.5	100.8	- 2.3
4	98.1	94	4.1	99.3	100.8	- 1.5
6	79.6	100	-20.4	80.5	93.8	-13.3
7	80.4	94	-13.6	80.0	86.3	- 6.3
8	80.3	92	-11.7	79.8	90.7	-10.9
9	75.7	83	- 7.2	74.1	84.3	- 7.2
10	77.1	92	-14.9	77.1	87.5	-10.4
11	95.2	119	-23.8	94.3	108.3	-14.0
12	103.7	139	-35.3	102.2	116.0	-13.8
13	104.2	134	-19.8	101.0	117.5	-16.5
14	95.2	107	-11.8	95.2	107.5	-12.3
15	80.3	104	-23.7	79.8	98.7	-18.9
16	81.6	95	-13.4	83.1	99.0	-15.9
17	91.9	101	- 9.1	81.9	97.8	-14.9
18	85.0	104	-19.0	87.2	97.5	-10.3
19	80.9	89	- 8.1	91.2	94.8	- 3.6
Mean	89.5	103.2	-14.3	88.9	98.6	- 9.8
Std. dev.	9.57	14.63	9.61	9.35	9.48	5.71
$\hat{t}$			-6.31			-7.27
sign.			0.0001			0.0001

Predicted diameters

Predicted and measured DBH are shown in Table IV, together with the residual (predicted - measured). The t-tests for the mean residuals indicate that they both are not significantly different than zero. Other tests were made to further compare the select and comparison-tree diameters.

1. A pairwise comparison of select and comparison-tree residuals shows the mean select residual to be greater, at a significance level of 0.025.
2. A comparison of two means of unequal sample sizes (18 select and 72 comparison residuals) gives the same conclusion, at a 0.090 level of significance. (The standard deviation of the 72 comparison tree residuals was 3.29.)

The results of the diameter measurements and comparisons were not as clear-cut as in the case of the heights. The most that can be said based on the statistical analysis is that, if there is a difference between the select and comparison tree diameters, it is small and is probably in the direction of the select trees' being larger then expected.

TABLE IV: Predicted diameters and diameter residuals (predicted - measured)

Plot	DBH of select trees (in.)			Mean DBH of comparison trees (in.)		
	Predicted	Measured	Residual	Predicted	Measured	Residual
1	17.5	19.5	-2.0	17.2	17.2	0.0
2	18.7	18.1	0.5	17.7	16.7	1.0
3	18.9	19.3	-0.4	18.1	17.5	0.5
4	15.9	14.8	1.1	17.0	16.1	0.9
6	15.3	13.9	1.4	14.5	12.8	1.7
7	14.9	14.4	0.5	13.7	11.9	1.8
8	13.7	14.7	-1.0	13.5	12.7	0.8
9	13.3	12.3	1.0	13.0	11.4	1.5
10	15.0	14.3	0.7	14.3	13.6	0.7
11	20.3	15.9	4.4	18.5	17.4	1.1
12	23.6	25.9	-2.3	19.8	18.5	1.3
13	22.1	23.0	-0.9	19.3	20.5	-1.2
14	17.5	17.9	-0.4	17.6	17.0	0.6
15	16.8	20.0	-3.2	16.0	17.8	-1.8
16	15.8	18.4	-2.6	16.5	17.1	-0.6
17	17.7	18.7	-0.9	16.7	16.9	-0.2
18	17.2	17.9	-0.7	16.3	17.3	-1.0
19	14.8	17.0	-1.1	16.2	16.6	-0.4
Mean	17.2	17.6	-0.4	16.4	16.1	0.4
Std. dev.	2.78	3.39	1.83	1.98	2.50	1.06
$\hat{t}$			-0.89			1.50
sign.			0.384			0.152

Reliability of regression equations

Table V presents the mean total height (measured heights of 4 comparison trees), height residual (predicted - measured), and residual as a percent of measured height for each of the 18 plots. Five of the plots (28%) had predicted heights within 5% of actual height; 7 plots (39%) were within 10%; 15 plots (83%) were within 15%; and all of the plots were within 20% of the measured height.

In an attempt to understand the reason for the consistent bias in the height predictions, predicted heights and residuals were calculated for the plot data of R. Marquard and J. Brown from which the regression equation had been developed. For 124 plots, the mean residual was -1.4 feet (standard deviation = 7.229). The calculated t-value was -2.18 (significance level = 0.031). When the residual was expressed as a percent of measured height, the corresponding values were: mean = -1.02%, std. dev. = 9.219, t = -1.23, significance level = 0.222.

Of the 124 plots, 44 (36%) had predicted heights within ±5% of measured height; 90 (73%) were within ±10%; 111 (90%) were within ±15%; 121 plots (98%) were within ±20%. The remaining three predictions were between 20% and 25% greater than the measured height.

In Table VI the corresponding values for the diameter predictions are given. Six plots (33%) had predicted diameters within ±5% of measured diameter; 14 plots (78%) were within ±10%; all 18 plots were within ±15% of measured diameter.

TABLE V: Reliability of height predictions.

Plot	Mean height (ft.)	Residual (ft.)	Residual (%)
1	97.0	-3.4	-3.5
2	100.5	-0.6	-0.6
3	100.8	-2.3	-2.3
4	100.8	-1.5	-1.5
6	93.8	-13.3	-13.2
7	86.3	-6.3	-7.3
8	90.7	-10.9	-12.0
9	81.3	-7.2	-8.8
10	87.5	-10.4	-11.9
11	108.3	-14.0	-12.9
12	116.0	-13.8	-11.9
13	117.5	-16.5	-14.1
14	107.5	-12.3	-11.4
15	98.7	-18.9	-19.2
16	99.0	-15.9	-16.1
17	97.8	-14.9	-15.2
18	97.5	-10.3	-10.5
19	94.8	-3.6	-3.8

TABLE VI: Reliability of diameter predictions.

Plot	Mean DBH (in.)	Residual (in.)	(%)
1	17.2	0.0	0.0
2	16.7	1.0	6.1
3	17.5	0.5	3.0
4	16.1	0.9	5.5
6	12.8	1.7	13.6
7	11.9	1.8	15.6
8	12.7	0.8	6.3
9	11.4	1.5	13.6
10	13.6	0.7	5.0
11	17.4	1.1	6.4
12	18.5	1.3	7.0
13	20.5	-1.2	-6.1
14	17.0	0.6	3.5
15	17.8	-1.8	-10.2
16	17.1	-0.6	-3.6
17	16.9	-0.2	-1.2
18	17.3	-1.0	-5.8
19	16.6	-0.4	-2.4

Correlations between branch size and other characteristics

Table VII shows simple correlation coefficients (R) between branch size and DBH, age, and height. Note that since branch size was rated on a scale of 1 to 4, smallest to largest, a positive correlation implies that "larger/older trees have bigger branches." Not surprisingly, all of the correlations of any significance are positive. The fact that there are no very high correlations is probably due to the fact that there are many other factors influencing branch size, both environmental and genetic.

The largest correlation is that between branch size and DBH for the select trees. During the selection process it was feared that there was some tendency to select slightly smaller trees because they had smaller branches. From the difference in branch size-DBH correlations for select and comparison trees, it appears that this did happen to some extent.

TABLE VII: Correlation between branch size and DBH, height, and age.

Correlation of branch size with:	Sample	Select trees	4-tree means	Comparison trees	All trees
	N	18	18	72	90
DBH	R	0.397	-0.055	0.291	0.305
	sign.	0.103	0.828	0.013	0.004
Height	R	0.192	0.053	0.190	0.184
	sign.	0.446	0.835	0.110	0.082
Age	R	0.058	0.298	0.148	0.126
	sign.	0.820	0.230	0.216	0.236

Correlations with basal area

Basal area around each tree was measured as an indicator of population density in order to determine if density influenced a tree's phenotype as "select" or "average." Table VIII presents simple correlation coefficients (R) between basal area and DBH, height, and age.

TABLE VIII: Simple correlation coefficients for BA with DBH, height, and age.

Correlation of BA with: \ Sample / N		Select trees 18	4-tree means 18	Comparison trees 72	All trees 90
DBH	R	-0.433	-0.344	-0.295	-0.324
	sign.	0.073	0.162	0.012	0.002
Height	R	-0.026	0.050	-0.044	-0.048
	sign.	0.920	0.845	0.712	0.652
Age	R	-0.042	0.010	0.025	0.010
	sign.	0.867	0.970	0.837	0.924

DISCUSSION

Analysis of the data gathered in this study indicates that the selection criteria used will yield trees that are taller, and perhaps larger in diameter as well, than an "average" tree would be expected to be. The residuals (predicted - measured) were consistently larger (more negative) for the select trees than for the comparison trees, although to a lesser extent in the case of diameter than height.

The bias in height predictions is difficult to explain. The 18 plots were in some of the same areas as were used to generate the equation, and those earlier plots show a much more balanced distribution of residuals (64 negative, 60 positive; see p. 22 for a summary).

Table IX gives a breakdown of height residuals from Marquard's plots in the three areas that I sampled from. Although they are not as balanced as the total set of 124 plots (especially at Tar Hollow), the pattern is much different than that of the 18 plots in the present study.

TABLE IX: Height residuals for 44 plots at Mohican, Tar Hollow, and Barnebey.

	Mohican	Tar Hollow	Barnebey	Total
N	18	15	11	44
Mean	0.305	-8.402	0.533	-4.891
Std. err.	1.016	1.851	2.999	2.877
t	0.300	-4.564	0.178	-1.700
sign.	0.768	0.001	0.862	0.096

It is quite possible that, considering the relatively small sample size, the 18 plots of this study did not represent the full range of site factors covered by the earlier study and that some combination of factors was missing, leading to the consistent underestimation of expected height. The DBH equation, however, uses a similar set of input variables, and no such deviation is apparent. One of the other equations developed by Marquard may give more even results, even if it has a lower R^2 value. I have not yet tried another one, though.

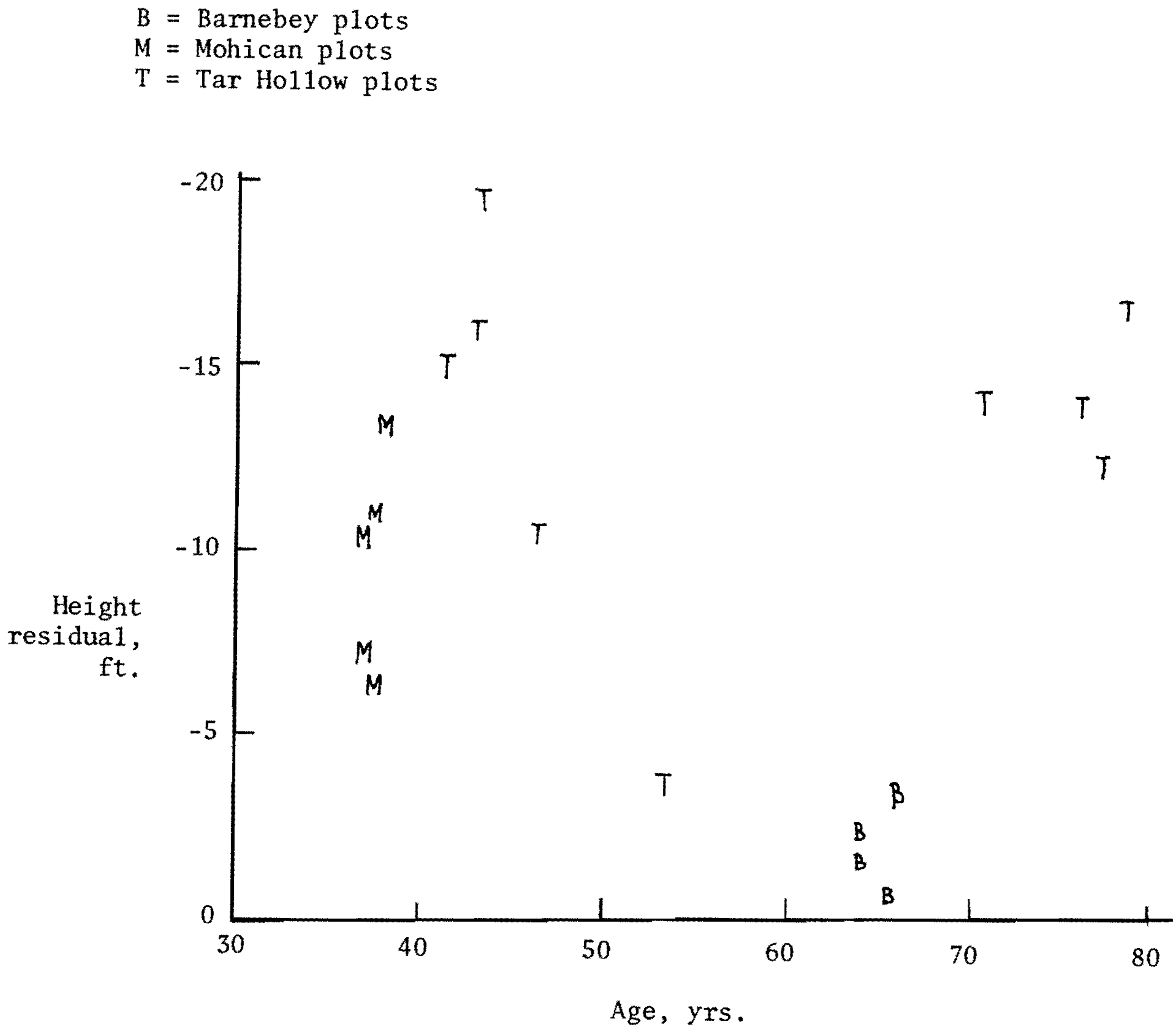
The plot mean ages in this study ranged from 37 to 78.5 (the two oldest select trees were 82 and 93), while the range in ages in Marquard's study was about 25 to 60. Because the relationships between height (or logarithm of height) are not exactly linear, applying the equation to trees 70 or 80 years old could result in a consistent error.

Figure 1 is a plot of height residuals (4-tree plot mean predicted minus measured) against mean age. It does not show any pattern of increasing error with age as might be expected.

Errors in the height measurements are another possible explanation (especially in plots 11-15, which were measured while the leaves were on the trees). However, it is difficult to accept this as a full explanation of the consistently negative residuals.

It is also possible that an effect discussed by Ledig (1974) is operating. He describes comparison-tree selection as a form of within-family selection (i.e., finding the best families, then choosing the best individual(s) within each of those families): "Because the greatest porportion of seed from a single tree falls within a short distance,

FIGURE 1: Height residuals (predicted - measured) vs. age.
(4-tree means)



many of the individuals in any small group could be half-sibs of each other...." I do not know to what extent this is true of yellow-poplar seeding in on old fields (or in a 40 year old plantation, as at Mohican). It may be, however, that the comparison trees used in this study were not randomly selected "average dominants or codominants," but were in effect "semi-superior" family relations of the select tree. It would be an interesting subject for further study to compare these trees with ones more distant in space and, perhaps, in family ties as well.

The less significant results of the DBH comparisons may be due to the effects of basal area, although BA did not seem to be very significant in the regression analysis. The correlations in Table VIII are significant only for BA with diameter, not with height; and the largest (negative) correlation is that with the select trees, raising the possible conclusion that the select trees are larger in diameter due to the effects of stand density. There are alternative explanations, including too small a sample size. It would take a more sophisticated statistical analysis, such as analysis of variance, to try to untangle the relationships between diameter, basal area, age, and site factors. That analysis is beyond the scope of this study.

It was for all practical purposes impossible to find one tree that scored best in all criteria. In particular, size and form were often in conflict, and it was sometimes difficult to separate superior form from youth. There are, however, significant differences in both form and size characteristics in the stands I studied, and these differences are reflected in the contrasts between select and comparison trees.

It must be emphasized, again, that a comparative study such as this one can draw no conclusions as to what growth and form characteristics the progenies of any of these would inherit. The genetic mechanisms of inheritance are complex, as are the interactions between genotype and environment that produce the trees we see.

In a narrow sense the height equation "failed" the reliability test and the diameter equation "passed." However, I think such conclusions would be premature, both because of the relatively small number of trees sampled in this study and because of the consistent differences between select and comparison residuals in both equations. Further sampling and testing would be neccessary to refine them.

A related topic for future study would be to predict the volume of timber in a stand from the expected heights and diameters, and compare that value with estimates from cruise data. If soil-site models for DBH and height can be used to estimate yields with less field work it would provide a valuable new tool for silviculture and forest management.

SUMMARY AND CONSLUSIONS

This comparative study showed phenotypic selection in even-aged yellow-poplar stands in southeastern Ohio to be effective in selecting larger than expected trees of superior form, without taking time-consuming age and height measurements. The results are only tentative, however, and more sampling would be required on a wider array of topographic positions.

The regression equations for predictiong height and diameter show potential for use in volume prediction. Further refinements and testing are neccessary, however, before such a procedure could become a practical management tool.

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APPENDIX

Guide for Selecting Stands of Yellow-poplar, _Liriodendron tulipifera_ L.

The OARDC selection program in yellow-poplar has as its ultimate objectives the genetic improvement of this species in growth rate and timber quality. One of the initial phases of the study is concerned with determining the extent of genetic gain possible through selection. Another task is to determine the most efficient method of selection.

To accomplish these initial goals, a state-wide survey of the range of genetic variation in growth rate and form of this species will be made. The stands selected will be used as seed collection areas for basic studies and, eventually, some of them may serve as a source of genetically superior seed for Ohio nurseries.

The stand selection program will serve as the basis for experiments to determine if family (stand) selection or individual tree selection is the most efficient means of obtaining genetic gain in growth rate and form. If stand selection is sufficient, the need for complex selection guides for selecting individual trees in uneven-aged mixed stands will be eliminated. The selected stands will also be used as permanent plots for growth studies and physiological observations. In addition, progeny test plantations established with seed collected from trees in these stands will provide excellent second-generation selection opportunities.

We are relying on the Service Forester in each Project Area to make the initial selections on the basis of their experience in the area. Owner cooperation is an important factor in selecting a stand. The selection project is designed so that harvest cuttings in the stands will not interfere with the objectives of the program, but clear-cutting or high grading would, of course, destroy the experimental value of the stands.

The initial selections should be made on the basis of the average phenotype of the stand, using the following criteria:

1. The stand must be located on a "good" site (relative to other sites in the area).

2. Yellow-poplar must be dominant or codominant in the stand. (Selected stands do not have to be pure stands of this species, as long as the yellow-poplar is one of the dominant components.)

3. If possible, selection should be based on the phenotype of trees in the 50 - 75 year age classes (i.e. young, vigorous, seed-bearing stands.) Each stand should provide three to five good-to-outstanding trees, each separated by 75 - 100 yards. Exceptions to this rule will be considered on an individual basis.

4. Cooperation of the landowner must be secured. None of our experimental operations will be of a destructive nature, but we will mark individual test trees from time to time.

We will need information on ownership, location, and approximate acreage of the stands. The OARDC will handle all subsequent measurement and seed collections. If additional information on the project is needed, contact:

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